Tactile Motion on the Glabrous Hand of Human and Non-Human Primates

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Tactile motion is a complex perceptual experience that requires a nervous system built from the ground up to allow rapid processing of spatial and temporal sensory information. Tactile motion relies primarily on Meissner corpuscles (RA-1), although Merkel cell-neurite complexes (SA-1) and Pacini corpuscles (RA-2) also play roles. Primary afferent projections from these receptors transmit sensory information to the brain in large fast fibers, and with high fidelity. The organization of primary somatosensory cortex is optimized for location and receptor type. Receptive fields of neurons in SI adapt with motion in order to increase feature selectivity. Neurons responding to motion, direction, and orientation can all be found in SI. Complex stimulus features, such as motion velocity, are resolved by population coding. Higher cortical areas for motion processing, such as the human motion complex (hMT+), are probably multisensory. Vision, in particular, seems to share motion processing architecture with the tactile modality. As in vision, tactile motion illusions may shed light on the cortical processing of motion, particularly when paired with functional imaging techniques. Apparent motion and the tactile motion aftereffect are two such illusions discussed in this review.

Keywords: *Somatosensation, motion perception, primates, humans*

In order to discuss tactile motion, it is first necessary to reveal the relevant biological pathways in cutaneous motion perception. The real action in tactile motion perception begins at the receptor surface of the somatosensory system, namely the skin. When the skin is deformed by physical stimulation, specialized mechanoreceptive neurons called primary afferent neurons are depolarized. This is possible because the terminal ends of these neurons contain mechanotransducer channels. These channels are normally closed but open when flexed. The exact mechanisms for this opening are varied[1-2] and are not as well characterized as the mechanically gated channels of stereocilia in cochlear hair cells[3]. The induced currents from open channels can be recorded from the cell soma in the dorsal root ganglion[4]. Upon mechanical stimulation, these channels open, and cations, such as Na^+ and Ca^{2+}, rush into the terminal. If the inward rush of positive current is sufficient, then an action potential is produced. This basic transduction mechanism underlies the broad spectrum of mechanical somatosensation, including motion.

Mechanoreceptors of motion

The wide range of sensory percepts experienced is due to different morphologies and anatomic locations of primary afferent terminals. In order to discuss motion on the glabrous skin of the hand, it is necessary to consider at least these afferent terminals: Meissner corpuscles, Merkel cell neurite complexes, and Pacinian corpuscles. These different mechanoreceptors are typically classified by their rate of adaptation to a stimulus. The rapidly adapting (RA) mechanoreceptors are Meissner corpuscles (RA-I) and Pacinian corpuscles (RA-II), whereas the slowly adapting (SA) mechanoreceptor is the Merkel cell neurite complex (SA-I). A second class of slowly adapting mechanoreceptors, Ruffini corpuscles (SA-II), are not present in the glabrous hand of the primate and exist only in tiny numbers in the glabrous hand of humans[5]. SA-I afferents terminate at Merkel cells at the base of the epidermis, the outermost layer of skin[6]. These afferents are densely populated in the glabrous skin of the hand, and provide precise localization and pressure information. RA-I afferents terminate in Meissner corpuscles just below the epidermis[7], are layered with specialized Schwann cells, and respond well to slip, flutter and motion. RA-II afferents terminate at the base of the dermis in Pacinian corpuscles[8] and respond preferentially to vibration. Each of these mechanoreceptor types contributes to motion in a unique way.

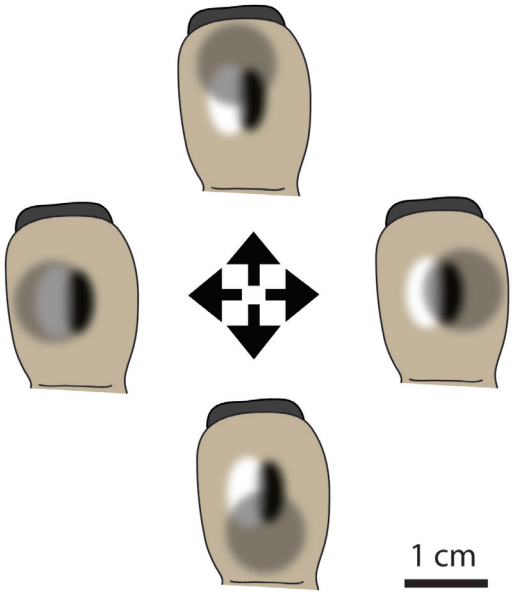

Figure 1: *Receptive fields as seen in Area 3b neurons.* On these four monkey fingertips, fixed excitatory (white), smaller fixed inhibitory (black) and larger lagged inhibitory (gray) receptive fields can be seen. The arrows in the center of the image signal the direction of a motion stimulus passing over the nearest fingerpad. The lagged inhibitory receptive field slides in the same direction as that of the motion stimulus, thereby modifying the overall receptive field. Note that these receptive fields are for illustration only and are not drawn to scale.

Dermatopic map:
A continuous repre-sentation of the somatic sensory surface, the skin. In this map, each fiber is beside the fiber that innervates the adjacent skin, and there are no breaks.

Somatotopic map:
A representation of body parts, some of which may be disconnected from the representation of adjacent skin areas. For example, the somatotopic map in primary somatosensory cortex has the thumb mapped next to the lower lip.

Modality:
A term that refers to the type of primary afferent, such as RA-1, SA-1, etc. Conservation of modality means that information from different primary afferent types stays segregated.

Mechanoreceptive afferent fibers can be individually recorded by microneurography[9-12]. This has allowed characterization of the output of the different mechanoreceptor types. This has also allowed direct measurement of receptive fields. Receptive field sizes for RA-I and SA-I fibers are 6.2mm and 4.8mm, respectively[13]. These receptive fields are not homogeneous, as they contain hotspots where some terminal branches are more sensitive than others[14]. For example, SA-I and RA-I fibers increase their firing rates linearly with indentation[15-16]. It was also discovered that making a second indentation in the skin just outside the receptive field produces a suppressive effect by means of relieving skin pressure in the receptive field[17].

Sensory transmission to the Central Nervous System

Mechanoreceptor afferent fibers are all large, myelinated A-beta fibers with conduction velocities between 36-73 m/s[18]. These properties are beneficial to rapid signal transmission to the central nervous system. Large-fibered mechanoreceptors project through the dorsal columns[19] of the spinal cord to the dorsal column nuclei. Dermatopy is preserved in the dorsal column, where sacral fibers are the most medial and cervical fibers are the most lateral[20-21]. These fibers rearrange before synapsing in the dorsal column nuclei, shifting from a dermatopic map to a somatotopic map[22]. The primate cuneate nucleus contains a complete somatotopic representation of the sensory surfaces of the hand[23].

Medial leminisal pathway. Under normal physiological conditions, dorsal column nuclei relay cells faithfully transmit the impulses of the primary afferent neurons[24-27].These cells project through the medial lemniscus to type I relay cells in the lateral division of the ventral posterior nucleus (VPN) of thalamus (Vc in humans). The VPN is also somatotopically organized[28-29]. The region of the VPN containing cutaneous afferents from the lemniscal tract projects to layers 4 and 3 of Areas 3b and 1 of somatosensory cortex[30].

Thalamus and SI cortex. Place and modality information are conserved from thalamus to Area 3b and 1[31], although signal transmission depends on vigilance. The amount of convergence from peripheral receptor to Area 3b is so restrained that Area 3b receptive field sizes are just 2-3 times the size of primary afferent receptive fields[32]. Dense microelectrode mapping demonstrates that there are somatotopic maps in areas 1 and 3b[33-34], demonstrating the

conservation of place information. The fingers representations in Area 1 and 3b point away from each other[35]. The hand representation can also be located histologically[36], or, in humans, anatomically[37-41] or by electrical cortical stimulation in waking humans[42-44]. These areas display a columnar structure[45], with different cortical columns representing different modalities, SA or RA[46].

All of the information so far illustrates that sensory information transduced by primary afferents in the skin is transmitted to cortex with high fidelity of place and modality information.

In some cases, primary afferent responses closely mimic psychophysical responses. For example, both primary afferent firing rates[15-16] and psychophysically perceived pressure[47] increase linearly with skin indentation. Another example is that RA-1 tactile thresholds match psychophysical thresholds[48-49]. Furthermore, a single impulse in a single RA-1 fiber from the fingerpad produces a tactile percept[12]. The cortex is essentially the bridge between stimulus transduction and tactile perception. Additional evidence linking cortical processing to this percept comes from finding BOLD response[50] and evoked potentials[51] from the same stimulus.

The rapidity and fidelity of tactile information, as noted above, allow for motion processing. If a finger is held on a surface without moving, spatial features of that surface are only weakly observed. However, even surface features a few microns tall can be perceived on a moving surface[52]. RA-1 afferents are thought to be responsible for this gain of function with movement[14,53]. This is especially true regarding slip of a smooth surface[54]. Because RA-1 afferents are silent when held motionless on a surface, only the SA-1 afferents collect useful information. When the surface is moved, the RA-1 and SA-1 afferents can respond to raised dots as small as 2-4 μm and 8 μm in height, respectively[52]. The detection of edges, as opposed to dots, is possible at sub-micron heights[55]. Interestingly, sensitivity does not change over a wide range of velocities (10-40 mm/s)[52]. However, optimal velocity ranges do differ depending on skin type and, presumably, receptor density. Essick et al.[56] showed that optimal velocities for motion to be perceived on the fingertip of humans ranged from 15 to 94 mm/s whereas for the proximal forearm the optimal velocities were 115-312 mm/s. Strokes of movement had to be 5.9 times longer on the forearm than on the fingertip in order to obtain the same sensitivity[56]. While increased force and velocity increase firing rate, the spatial pattern of firing does not change[57].

Cortical processing of motion

Primary somatosensory cortex processes basic sensory input to reveal complex features. One important cortical process is to use population coding. For example, localization discrimination thresholds on the fingertip can be as low as 0.38 mm for a 1.9 mm tactile probe[58]. Although there is overlap in the area that the probe depresses in such intervals, the population responses are different enough to discriminate. Significantly, this discrimination threshold is smaller than the receptive fields of single primary afferents. Other complex percepts, such as curvature, orientation, movement, and direction, also require population coding.

Receptive fields of Area 3b neurons have been described in detail[32,59-61]. 95% of these neurons have an excitatory field of about 24 mm^2 on the skin, with a range of 3-43 mm^2. However, about 5% of 3b cells in the same study had two or more excitatory receptive field regions. They also have an adjacent inhibitory field of about 18 mm^2, with a range of 1-47 mm^2. This configuration enhances feature contrast and preference. Remarkably, there is also a dynamic, delayed inhibitory field, whose position is not fixed, but rather biases in the direction of motion[32]. The 30 ms delay of this inhibitory field could serve to suppress minor features in the scanning direction on smooth surfaces and to emphasize novelty. At sufficient scanning speeds, it may even serve to confer directional

Orientation:
A cell is said to have orientation preference if its preferred stimulus passes through the receptive field at a specific angle, regardless of direction.

Motion:
A cell is said to have motion preference if its preferred stimulus moves through the receptive field at any angle and direction.

Direction:
A cell is said to have direction preference if its preferred stimulus moves through the receptive field in one direction, but not the opposite direction.

Intrinsic optical imaging: This functional imaging technique collects backscattered light from the cortex and detects metabolic activity as oxygen-deficient hemoglobin absorbs more light than oxygen-rich hemoglobin.

preference[61]. Thus, Area 3b is the first stage of processing in the somatosensory system known to process motion.

Cortical neurons in Areas 3b, 1, and 2 are known to be sensitive to direction (60%), motion (37%), and orientation (3%)[62]. These cells are evenly split between RA type and SA type receptive fields[63]. Motion cells are mostly located in Area 3b, whereas direction cells are mostly located in Areas 1 and 2. Most of this processing seems to occur in layer 3, as opposed to layer 4 where most thalamic projections terminate[64]. Direction variant cells have also been found[65-67]. These cells respond to stimulus movement toward or away from a specific spot in the receptive field, typically located over a joint. Although primary somatosensory cortex (SI) has a broad variety of motion sensitivity, the higher-level characteristics of motion, such as velocity, appear to be processed in higher cortical areas.

Motion processing is thought to follow the dorsal pathway, which is used to guide movements. A number of imaging studies have implicated inferior parietal lobe and the human motion complex (hMT+)[68-71], although it has been proposed that the medial superior temporal area (MST) rather than the middle temporal area (MT) processes tactile motion[72]. Area hMT+ is best known for its role in visual motion processing. However, thanks to functional lesion studies with repetitive Transcranial Magnetic Stimulation (rTMS), it also appears to be necessary for tactile motion speed perception[73-74]. In order to deduce whether the area is truly multisensory or not, several studies have looked at combined visual and tactile motion paradigms. Results have included findings of facilitation between modalities[75] as well as interference between modalities[76-77]. These studies imply that there are shared resources for visual and tactile motion, lending further support to the idea that hMT+ is a multisensory motion processing area.

Motion Illusions

One of the major goals of cortical studies of motion is to uncover the neural correlates of perception. One way to study this is to use illusions in order to dissociate perception from reality. If the cortical area follows the real stimulus instead of the perceptual experience, then the area is not implicated in the illusory processing. Since many complex cortical processes use population coding, studying such processes at the single neuron level is unfeasible. Imaging methods are much better suited to study population coding, as they can look at processing within or between areas. Intrinsic optical imaging and functional Magnetic Resonance Imaging (fMRI) have been used to study the funneling illusion, finding that Area 3b activation reflects the perceived location rather than the somatotopic location[78-80].

Several interesting tactile motion illusions exist and have been psychophysically characterized. One of these is apparent motion. Apparent motion is perceived motion created by sequential discrete tactile stimulations on spatially disparate skin locations. The spatial pattern of stimulation and type of movement (expanding, contracting, etc) have little effect on the saliency of the apparent motion, but the optimal range of inter-stimulus intervals varies with stimulus duration[81,82]. The cortical mechanisms of apparent motion are not fully understood, but methods are being developed to probe this question with intrinsic optical imaging and fMRI[83-84]. These techniques offer the wide field of view necessary to study population coding. However, they sacrifice considerable spatial resolution in doing so. One promising technology that could be applied to tactile motion imaging is voltage sensitive dye imaging[85]. This technique has already been applied to visual motion[86] and offers temporal resolution on the order of milliseconds. For a rapidly developing, complex stimulus such as motion, such a technique may be necessary to understand the mechanisms of cortical motion processing.

Another promising tactile motion illusion is the motion aftereffect (MAE). By generating a

continuous motion stimulus for a period of time (up to several minutes) and suddenly removing the stimulus, a tactile motion sensation in the other direction is produced[87-89]. This is very similar to the visual motion aftereffect. In fact, Konkle et al.[90] found that the aftereffect can transfer between tactile and visual modalities. This further suggests the existence of shared processing for motion in the two modalities. The tactile MAE is probably conferred through RA-1 afferents, as it is much more difficult to evoke in skin locations with a lower innervation density of these fibers[91]. There are now tactile MAE paradigms designed specifically to elicit the best responses from RA-1 afferents[92]. Interestingly, the tactile MAE is produced even with apparent motion across crossed digits[93]. This means that the tactile MAE reflects environmental space as opposed to tactile space. The cortical correlates of this illusion are unknown, but a recent fMRI investigation shows that only SI remains active during the illusion[94], suggesting a functional role in the illusion.

The biological study of tactile motion seems to be entering a new era. Whereas microneurography and single-unit electrophysiology still dominated the field at the turn of the 21st century, the pendulum is swinging towards studies of population dynamics in relatively large cortical areas. Imaging methods, such as voltage sensitive dye imaging, offer a larger scope on cortical processing. The presence of two robust tactile illusions may prove to be critical for dissociating sensory and perceptual processing.

References

1. Lumpkin EA and Caterina MJ (2007). Mechanisms of sensory transduction in the skin. Nature. 445: 858–865.

2. Delmas P, Hao J and Rodat-Despoix L (2011). Molecular mechanisms of mechanotransduction in mammalian sensory neurons. Nat Rev Neurosci. 12: 139–153.

3. Gillespie PG (1995). Molecular machinery of auditory and vestibular transduction. Current Opinion in Neurobiology. 5: 449–455.

4. McCarter GC, Reichling DB and Levine JD (1999). Mechanical transduction by rat dorsal root ganglion neurons in vitro. Neurosci Lett. 273: 179–182.

5. Paré M, Behets C and Cornu O (2003). Paucity of presumptive ruffini corpuscles in the index finger pad of humans. J Comp Neurol. 456: 260–266.

6. Merkel F (1875). Tastzellen und Tastkörperchen bei den Hausthieren und beim Menschen. Archiv f. mikrosk. Anat. 11: 636–652.

7. Meissner G (1853). Beitrage zur Anatomie und Physiologie der Haut, Leipzig:Leopold Voss.

8. Pacini F (1840). Nuovi organi scoperti nel corpo umano, Pistoia:Tipografia Cino.

9. Vallbo AB and Hagbarth KE (1967). Impulses recorded with micro-electrodes in human muscle nerves during stimulation of mechanoreceptors and voluntary contractions. Electroencephalogr Clin Neurophysiol. 23: 392 (1967).

10. Vallbo AB, Hagbarth KE and Wallin BG (2004). Microneurography: how the technique developed and its role in the investigation of the sympathetic nervous system. J Appl Physiol. 96: 1262–1269.

11. Vallbo AB and Johansson RS (1984). Properties of cutaneous mechanoreceptors in the human hand related to touch sensation. Human neurobiology. 3: 3–14.

12. Torebjörk HE, Vallbo AB and Ochoa JL (1987). Intraneural microstimulation in man. Its relation to specificity of tactile sensations. Brain. 110 (6): 1509–1529.

13. Phillips JR, Johansson RS and Johnson KO (1992). Responses of human mechanoreceptive afferents to embossed dot arrays scanned across fingerpad skin. Journal of Neuroscience. 12: 827–839.

14. Gardner EP and Palmer CI (1989). Simulation of motion on the skin. II. Cutaneous mechanoreceptor coding of the width and texture of bar patterns displaced across the OPTACON. J Neurophysiol. 62: 1437–1460.

15. Vega-Bermudez F and Johnson KO (1999). SA1 and RA receptive fields, response variability, and population responses mapped with a probe array. J Neurophysiol. 81: 2701–2710.

16. Vega-Bermudez F and Johnson KO (1999). Surround suppression in the responses of primate SA1 and RA mechanoreceptive afferents mapped with a probe array. J Neurophysiol. 81: 2711–2719.

17. Phillips JR and Johnson KO (1981). Tactile spatial resolution. III. A continuum mechanics model of skin predicting mechanoreceptor responses to bars, edges, and gratings. J Neurophysiol. 46: 1204–1225.

18. Kakuda N (1992). Conduction velocity of low-threshold mechanoreceptive afferent fibers in the glabrous and hairy skin of human hands measured with microneurography and spike-triggered averaging. Neurosci Res. 15: 179–188.

19. Head H and Holmes G (1911). Sensory disturbances from cerebral lesions. Brain. 34: 102–254.

20. Walker AE and Weaver TA (1942). The topical organization and termination of the fibers of the posterior columns in Macaca mulatta. J Comp Neurol. 76: 145–158.

21. Chang HT and Ruch TC (1947). Organization of the dorsal columns of the spinal cord and their nuclei in the spider monkey. J Anat. 81: 140–149.

22. Whitsel BL, Petrucelli LM, Sapiro G and Ha H (1970). Fiber sorting in the fasciculus gracilis of squirrel monkeys. Exp Neurol. 29: 227–242.

23. Florence SL, Wall JT and Kaas JH (1989). Somatotopic organization of inputs from the hand to the spinal gray and

cuneate nucleus of monkeys with observations on the cuneate nucleus of humans. J Comp Neuro.l. 286: 48–70.

24. Ferrington DG, Rowe MJ and Tarvin RP (1987). Actions of single sensory fibres on cat dorsal column nuclei neurones: vibratory signalling in a one-to-one linkage. The Journal of physiology. 386: 293–309.

25. Ferrington DG, Rowe MJ and Tarvin RP (1987). Integrative processing of vibratory information in cat dorsal column nuclei neurones driven by identified sensory fibres. The Journal of physiology. 386: 311–331.

26. Greenstein J, Kavanagh P and Rowe MJ (1987). Phase coherence in vibration-induced responses of tactile fibres associated with Pacinian corpuscle receptors in the cat. The Journal of physiology. 386: 263–275.

27. Douglas PR, Ferrington DG and Rowe M (1978). Coding of information about tactile stimuli by neurones of the cuneate nucleus. The Journal of physiology. 285: 493–513.

28. Mountcastle VB and Henneman E (1952). The representation of tactile sensibility in the thalamus of the monkey. J Comp Neurol. 97: 409–439.

29. Lenz FA, Dostrovsky JO, Tasker RR, Yamashiro K, Kwan HC and Murphy JT (1988). Single-unit analysis of the human ventral thalamic nuclear group: somatosensory responses. J Neurophysiol. 59: 299–316.

30. Jones EG and Friedman DP (1982). Projection pattern of functional components of thalamic ventrobasal complex on monkey somatosensory cortex. J Neurophysiol. 48: 521–544.

31. Jones EG, Friedman DP and Hendry SH (1982). Thalamic basis of place- and modality-specific columns in monkey somatosensory cortex: a correlative anatomical and physiological study. J Neurophysiol. 48: 545–568.

32. **DiCarlo JJ and Johnson KO (2000). Spatial and temporal structure of receptive fields in primate somatosensory area 3b: effects of stimulus scanning direction and orientation. J Neurosci. 20: 495–510.**

This paper provides the best description of area 3b receptive fields. It is also the first to explain the lagged inhibitory field that biases in the direction of motion.

33. Paul RL, Goodman H and Merzenich M (1972). Alterations in mechanoreceptor input to Brodmann's areas 1 and 3 of the postcentral hand area of Macaca mulatta after nerve section and regeneration. Brain Res. 39: 1–19.

34. Paul RL, Merzenich M and Goodman H (1972). Representation of slowly and rapidly adapting cutaneous mechanoreceptors of the hand in Brodmann's areas 3 and 1 of Macaca mulatta. Brain Res. 36: 229–249.

35. Kaas JH (1987). The Organization of Neocortex in Mammals: Implications for Theories of Brain Function. Annual review of psychology. 38: 129–151.

36. Jain N, Catania KC and Kaas JH (1998). A histologically visible representation of the fingers and palm in primate area 3b and its immutability following long-term deafferentations. Cereb Cortex. 8: 227–236.

37. Cunningham DJ (1982). Contribution to the surface anatomy of the cerebral hemispheres, Dublin: Academy House.

38. White LE, Andrews TJ, Hulette C, Richards A, Groelle M, Paydarfar J and Purves D (1997). Structure of the human sensorimotor system. I: Morphology and cytoarchitecture of the central sulcus. Cereb Cortex. 7: 18–30.

39. White LE, Andrews TJ, Hulette C, Richards A, Groelle M, Paydarfar J and Purves D (1997). Structure of the human sensorimotor system II: Lateral symmetry. Cereb Cortex. 7: 31–47.

40. Sastre-Janer FA, Regis J, Belin P, Mangin JF, Dormont D, Masure MC, Remy P, Frouin V and Samson Y (1998). Three-dimensional reconstruction of the human central sulcus reveals a morphological correlate of the hand area. Cereb Cortex. 8: 641–647.

41. Yousry TA, Schmid UD, Alkadhi H, Schmidt D, Peraud A, Buettner A and Winkler P (1997). Localization of the motor hand area to a knob on the precentral gyrus. A new landmark. Brain. 120 (Pt 1): 141–157.

42. Cushing H (1909). A note upon the faradic stimulation of the postcentral gyrus in conscious patients. Brain. 32: 44–53.

43. Foerster O (1936). The motor cortex in man in the light of Hughlings Jackson's doctrines. Brain. 59: 135–159.

44. Penfield W and Jasper HH (1954). Epilepsy and the functional anatomy of the human brain, Boston: Little, Brown.

45. Mountcastle VB (1997). The columnar organization of the neocortex. Brain. **120** (Pt 4): 701–722.

46. Sur M, Wall JT and Kaas JH (1984). Modular distribution of neurons with slowly adapting and rapidly adapting responses in area 3b of somatosensory cortex in monkeys. J Neurophysiol. 51: 724–744.

47. Stevens SS (1970). Neural Events and the Psychophysical Law: Power functions like those that govern subjective magnitude show themselves in neurelectric effects. Science. 170: 1043–1050.

48. Johansson RS and Vallbo AB (1979). Detection of tactile stimuli. Thresholds of afferent units related to psychophysical thresholds in the human hand. The Journal of physiology. 297: 405–422.

49. Johansson RS and Vallbo AB (1979). Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. The Journal of physiology. 286: 283–300.

50. Trulsson M, Francis ST, Kelly EF, Westling G, Bowtell R and McGlone F (2001). Cortical responses to single mechanoreceptive afferent microstimulation revealed with fMRI. Neuroimage. 13: 613–622.

51. Kunesch E, Knecht S, Schnitzler A, Tyercha C, Schmitz F and Freund HJ (1995). Somatosensory evoked potentials elicited by intraneural microstimulation of afferent nerve fibers. Journal of clinical neurophysiology. 12: 476–487.

52. LaMotte RH and Whitehouse J (1986). Tactile detection of a dot on a smooth surface: peripheral neural events. J Neurophysiol. 56: 1109–1128.

53. Gardner EP and Palmer CI (1989). Simulation of motion on the skin. I. Receptive fields and temporal frequency coding by cutaneous mechanoreceptors of OPTACON pulses delivered to the hand. J Neurophysiol. 62: 1410–1436.

54. Srinivasan MA, Whitehouse JM and LaMotte RH (1990). Tactile detection of slip: surface microgeometry and peripheral neural codes. J Neurophysiol. 63: 1323–1332.

55. Johansson RS and LaMotte RH (1983). Tactile detection thresholds for a single asperity on an otherwise smooth surface. Somatosens Res. 1: 21–31.

56. Essick GK, Bredehoeft KR, McLaughlin DF and Szaniszlo JA (1991). Directional sensitivity along the upper limb in humans. Somatosens Mot Res. 8: 13–22.

57. Edin B, Essick G, Trulsson M and Olsson K (1995). Receptor encoding of moving tactile stimuli in humans. I. Temporal pattern of discharge of individual low-threshold mechanoreceptors. J Neurosci. 15: 830–847.

58. Wheat HE, Goodwin AW and Browning AS (1995). Tactile resolution: peripheral neural mechanisms underlying the human capacity to determine positions of objects contacting the fingerpad. Journal of Neuroscience. 15: 5582–5595.

59. DiCarlo JJ, Johnson KO and Hsiao SS (1998). Structure of receptive fields in area 3b of primary somatosensory cortex in the alert monkey. Journal of Neuroscience. 18: 2626–2645.

60. DiCarlo JJ and Johnson KO (1999). Velocity invariance of receptive field structure in somatosensory cortical area 3b of the alert monkey. Journal of Neuroscience. 19: 401–419.

61. DiCarlo JJ and Johnson KO (2002). Receptive field structure in cortical area 3b of the alert monkey. Behav Brain Res. 135: 167–178.

62. **Warren S, Hämäläinen HA and Gardner EP (1986). Objective classification of motion- and direction-sensitive neurons in primary somatosensory cortex of awake monkeys. J Neurophysiol. 56 (3): 598-622.**

This paper was the first to describe orientation cells in SI. It also contains great characterizations of movement and direction cells.

63. Ruiz S, Crespo P and Romo R (1995). Representation of moving tactile stimuli in the somatic sensory cortex of awake monkeys. J Neurophysiol. 73 (2): 525-537.

64. Whitsel BL, Roppolo JR and Werner G (1972). Cortical information processing of stimulus motion on primate skin. J Neurophysiol. 35: 691–717.

65. Essick GK and Whitsel BL (1985). Factors influencing cutaneous directional sensitivity: a correlative psychophysical and neurophysiological investigation. Brain Res. 357: 213–230.

66. Pei YC, Hsiao SS, Craig JC and Bensmaia SJ (2010). Shape invariant coding of motion direction in somatosensory cortex. PLoS Biol. 8: e1000305.

67. Pei YC, Hsiao SS and Bensmaïa SJ (2008). The tactile integration of local motion cues is analogous to its visual counterpart. Proceedings of the National Academy of Sciences. 105: 8130–8135.

68. Francis S, Summers I, Clemence M, McGlone F, Chanter C and Bowtell R (2001). An fMRI study of brain activation due to tactile motion. Neuroimage. 13: S1166.

69. Hagen MC, Franzén O, McGlone F, Essick G, Dancer C and Pardo JV (2002). Tactile motion activates the human middle temporal/V5 (MT/V5) complex. Eur J Neurosci. 16: 957–964.

70. Summers IR, Francis ST, Bowtell RW, McGlone FP and Clemence MA (2009). Functional-magnetic-resonance-imaging investigation of cortical activation from moving vibrotactile stimuli on the fingertip. J Acoust Soc Am. 125: 1033–1039.

71. Wacker E, Spitzer B, Lützkendorf R, Bernarding J and Blankenburg F (2011). Tactile motion and pattern processing assessed with high-field FMRI. PLoS ONE. 6: e24860.

72. Beauchamp MS, Yasar NE, Kishan N and Ro T (2007). Human MST but not MT responds to tactile stimulation. J Neurosci. 27: 8261–8267.

73. Ricciardi E, Basso D, Sani L, Bonino D, Vecchi T, Pietrini P and Miniussi C (2011). Functional inhibition of the human middle temporal cortex affects non-visual motion perception: a repetitive transcranial magnetic stimulation study during tactile speed discrimination. Exp. Biol. Med. (Maywood). 236: 138–144.

74. Basso D, Pavan A, Ricciardi E, Fagioli S, Vecchi T, Miniussi C and Pietrini P (2012). Touching Motion: rTMS on the Human Middle Temporal Complex Interferes with Tactile Speed Perception. Brain topography (epub ahead of print).

75. Gori M, Mazzilli G, Sandini G and Burr D (2011) Cross-Sensory Facilitation Reveals Neural Interactions between Visual and Tactile Motion in Humans. Front Psychol 2: 55.

76. Craig JC (2006). Visual motion interferes with tactile motion perception. Perception. 35: 351–367.

77. Bensmaïa SJ, Killebrew JH and Craig JC (2006). Influence of visual motion on tactile motion perception. J Neurophysiol. 96: 1625–1637.

78. Chen LM, Friedman RM and Roe AW (2003). Optical imaging of a tactile illusion in area 3b of the primary somatosensory cortex. Science. 302: 881–885.

79. Chen LM, Turner GH, Friedman RM, Zhang N, Gore JC, Roe AW and Avison MJ (2007). High-resolution maps of real and illusory tactile activation in primary somatosensory cortex in individual monkeys with functional magnetic resonance imaging and optical imaging. J Neurosci. 27: 9181–9191.

80. Roe AW and Chen LM (2008). High-resolution fMRI maps of cortical activation in nonhuman primates: correlation with intrinsic signal optical images. ILAR J. 49: 116–123.

81. Kirman J (1974). Tactile apparent movement: The effects of interstimulus onset interval and stimulus duration. Percept Psychophys. 1–6.

82. Kirman JH (1983). Tactile apparent movement: the effects of shape and type of motion. Percept Psychophys. 34: 96–102.

83. Peelen MV, Rogers J, Wing AM, Downing PE and Bracewell RM (2010). Unitary haptic perception: integrating moving tactile inputs from anatomically adjacent and non-adjacent digits. Experimental Brain Research. 204: 457–464.

84. **Friedman RM, Dillenburger BC, Wang F, Avison MJ, Gore JC, Roe AW and Chen LM (2011). Methods for fine scale functional imaging of tactile motion in human and nonhuman primates. Open Neuroimag J. 5: 160–171.**

This paper lays the groundwork for studying tactile motion perception with functional imaging methods, including fMRI and intrinsic optical imaging. These methods are promising because they can be used to study population responses in cortex.

85. Grinvald A and Hildesheim R (2004). VSDI: a new era in functional imaging of cortical dynamics. Nat Rev Neurosci. 5: 874–885.

86. Onat S, Nortmann N, Rekauzke S, Konig P and Jancke D (2011). Independent encoding of grating motion across stationary feature maps in primary visual cortex visualized with voltage-sensitive dye imaging. Neuroimage 55: 1763–1770.

87. **Hollins M and Favorov O (1994). The Tactile Movement Aftereffect. Somatosens Mot Res. 11: 153–162.**

This paper describes the first successful method for presenting a tactile motion aftereffect. This aftereffect may prove useful in studying perceptual experience in primate cortex.

88. Lerner EA and Craig JC (2002). The prevalence of tactile motion aftereffects. Somatosens Mot Res. 19: 24–29.

89. Planetta PJ and Servos P (2008). The tactile motion aftereffect revisited. Somatosens Mot Res. 25: 93–99.

90. Konkle T, Wang Q, Hayward V and Moore CI (2009). Motion aftereffects transfer between touch and vision. Curr Biol. 19: 745–750.

91. Planetta PJ and Servos P (2010). Site of stimulation effects on the prevalence of the tactile motion aftereffect. Experimental Brain Research. 202: 377–383.

92. Watanabe J, Hayashi S, Kajimoto H, Tachi S and Nishida S (2007). Tactile motion aftereffects produced by appropriate presentation for mechanoreceptors. Experimental Brain Research. 180: 577–582.

93. Kuroki S, Watanabe J, Mabuchi K, Tachi S and Nishida S (2011). Directional remapping in tactile inter-finger apparent motion: a motion aftereffect study. Experimental Brain Research. 216: 311–320.

94. Planetta PJ and Servos P (2011). The postcentral gyrus shows sustained fMRI activation during the tactile motion aftereffect. Experimental Brain Research. 216: 535–544.

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Further information: http://www.psy.vanderbilt.edu/faculty/roeaw/index.html